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THE GENERA OF RUTACEAE IN THE SOUTHEASTERN UNITED STATES [1]

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RUTACEAE Jussieu, Gen. Pl. 296. 1789.

(RUE FAMILY)

Armed or unarmed trees or shrubs [sometimes scandent or xeromorphic], rarely herbs. Leaves alternate or more rarely opposite, simple or compound, usually glandular-punctate at least at the margin, exstipulate; petioles sometimes winged. Flowers bisexual and/or unisexual, the plants monoecious, dioecious, or polygamous, regular [rarely irregular], usually 3–5-merous, the insertion hypogynous, solitary and axillary or in various axillary or terminal, often cymose, inflorescences. Sepals distinct or connate, very rarely wanting, often glandular-dotted, usually imbricate in bud. Petals distinct [rarely connate or wanting], often glandular-dotted, imbricate or valvate. Stamens as many as the petals and in 1 series (haplostemonous) or twice as many to more numerous and in 2 series (diplo- or obdiplostemonous), those of the outer series often shorter than those of the inner [or occasionally reduced to staminodes]; filaments distinct or ± connate, often conspicuously dilated [or rarely appendaged] at base; anthers versatile, introrse, 2[4]-locular at anthesis, often gland-tipped, longitudinally dehiscent. Intrastaminal nectariferous disc ring-, cup-, or cushion-like, rarely wanting. Gynoecium of (1)2–5(–several),

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University which has been made possible through the support of George R. Cooley and the National Science Foundation. This treatment follows the pattern established in the first paper in the series (Jour. Arnold Arb. 39: 296–346. 1958) and continued through those in volumes 40–42 (1959–1961). It should be repeated that the area covered by this work is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with any supplementary material in brackets. References which the author has not seen are marked by an asterisk.

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sessile or stipitate, distinct or incompletely to completely connate carpels; stigmas simple or lobed; styles basal, ± lateral or terminal, distinct, connivent or connate; ovaries 1-locular or 2–5(–several) locular, with axile placentae [very rarely 1-locular with parietal placentae]; ovules usually anatropous and epitropous [rarely apotropous], with 2 integuments and a thick nucellus, 1 or 2–many in each locule of the ovary. Fruit of (1)2–5(–several) follicles or drupes, or a capsule, berry, drupe, samara, or schizocarp; pericarp often glandular-pitted to -verruculose. Seeds with or without endosperm, sessile or funiculate, 1 or 2–several in a locule; embryo relatively large, straight or curved, with plano-convex, sometimes convolute [rarely plicate] cotyledons and a superior radicle. TYPE GENUS: *Ruta* L.

A family of about 150 genera and 1600 species, widely distributed in tropical and temperate regions, most abundant in tropical America, South Africa, and Australia, extremely scarce in Europe. Eight genera (five naturalized) in three subfamilies are represented in our area.

The presence of secretory cavities (or at least inner multicellular glands) containing an aromatic volatile oil in stems (in cortex, rarely in phloem), leaves, floral parts, and pericarp of fruits is a characteristic feature of the family, distinguishing Rutaceae from their morphologically very similar allies, especially Simaroubaceae and Meliaceae. Rutaceae are also closely related to Zygophyllaceae, Cneoraceae, and Burseraceae.

The family, in general, seems to be entomophilous, insects being attracted by the strong smell of the flowers and/or by usually abundant nectar, sometimes also by showy corollas (e.g., *Citrus* spp.). Ornithophilly has also been presumed for some genera. Cross-pollination seems to be the rule. In some genera self-pollination is prevented by dicliny, or (in monoclinous genera) by proterandry (e.g., *Ruta*, *Ravenia*, *Barosma*) and/or the position of the stigma in regard to the anthers (e.g., *Triphasia*, *Dictamnus*). In some genera, however, both cross- and self-pollination seem equally possible and effective (e.g., *Choisya*, *Skimmia*, *Murraya*, *Poncirus*, *Citrus*). Cleistogamy has been recorded in the New Zealand *Melicope simplex* A. Cunn. Nucellar embryony (apomixis) has been shown in several genera (e.g., *Zanthoxylum*, *Esenbeckia*, *Ptelea*(?), *Triphasia*, *Aegle*, *Murraya*, *Poncirus*, *Citrus*), but probably is of even wider distribution in the family. Zygotic (gametic) polyembryony seems to be very rare, having been recorded or presumed in only a few cases.

Chromosome counts have been made for about 50 genera and 150 species. On the basis of these counts, nine appears to be a basic number for the family. (Banerji [1954], however, suggested three as a basic number and nine as a result of secondary polyploidy for *Citrus grandis* (L.) Osbeck.) The family, in general, appears to be ± euploid, except the Australian aneuploid tribe Boronieae (which has chromosome numbers based on 7, 8, 9, 11, 13, 17, 19) and apparently some genera from other tribes. Polyploidy is widely distributed in Rutaceae and seems to be of importance in the evolutionary development of the family.

The family is of economic importance, notably for a number of important fruits (*Citrus* spp., *q.v.*), timbers, aromatic oils (e.g., *Citrus* spp., *Ruta graveolens* L.), various products of medicinal value, and ornamentals.

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KEY TO THE GENERA OF RUTACEAE

General characters: *leaves usually pinnate to 3–1-foliolate, alternate, rarely opposite; leaflets (at least at margin), perianth parts, and fruits glandular-, often pellucid-punctate.*

A. Plant a perennial herb or subshrub; leaves 2- to 3-pinnately divided; flowers greenish yellow, bisexual, 4–5-merous with 8–10 stamens; fruits 5-lobed, many-seeded capsules. ..... 1. *Ruta.*

A. Plants woody, shrubs or trees.

B. Flowers unisexual or uni- and bisexual, small, yellowish or yellowish white, 3–5-merous, sometimes without calyx; stamens as many as petals; gynoecium apo- or syncarpous, (1)2–5-carpellate; fruits dry; leaves alternate.

C. Plants dioecious or monoecious, often prickly; leaves pinnate, usually 5 or more foliolate; flowers unisexual, with or without sepals; gynoecium apocarpous, (1)2–5-carpellate; fruits dehiscent, 1-seeded follicles. ..... 2. *Zanthoxylum.*

C. Plants polygamous, unarmed; leaves usually 3-foliolate; flowers uni- and bisexual; gynoecium syncarpous, 2-loculate; fruit a flat, indehiscent, 2-locular, 2-winged samara. ..... 3. *Ptelea.*

B. Flowers usually bisexual, small to large, usually white, 3–5-merous; stamens twice as many as petals, or more numerous; gynoecium syncarpous, 2–18-locular, rarely 1-carpellate; fruits fleshy drupes or berries; leaves alternate or opposite.

D. Stamens twice as many as petals; flowers relatively small; ovary 1–5-loculate; fruits small, pulp without pulp-vesicles; petioles not winged.

E. Ovary 1-carpellate; fruit a 1-seeded drupe; leaves opposite, 3-foliolate; flowers usually 4-merous, paniculate; unarmed, aromatic, resinous shrubs or trees. ..... 4. *Amyris.*

E. Ovary 2–5-carpellate; fruit a 1–3-seeded berry; leaves alternate.

F. Flowers (4)5-merous, in short, spikelike axillary panicles; berry subglobular, sometimes depressed at apex and slightly oblique, white to pink, 1–3-seeded, edible; unarmed shrubs or trees with pinnate, usually 1–3(5)-foliolate leaves and large leaflets. ..... 5. *Glycosmis.*

F. Flowers usually 3-merous, solitary or in 2's or 3's in the leaf axils; berry subglobular, sometimes apiculate, reddish orange to crimson, 1–3-seeded, insipid; shrubs with solitary or paired, axillary spines; leaves 3-foliolate, leaflets small. . . . . 6. *Triphasia.*

D. Stamens numerous (20–60); flowers relatively large; perianth usually 5-merous; ovary 6–18-loculate; fruits (hesperidia) greenish yellow, yellow, orange to reddish orange, large, pulp formed by pulp vesicles; usually thorny shrubs or trees, mostly with winged petioles.

G. Flowers on the previous year's branchlets; stamens distinct; ovary 6–8-loculate; fruits relatively large, pubescent, pulp with very sour and acrid juice; leaves 3-foliolate, deciduous. . . . 7. *Poncirus.*

G. Flowers on new branchlets; stamens polyadelphous; ovary 8–18-loculate; fruits large, glabrous, pulp with sweet or sour not acrid juice; leaves 1-foliolate, persistent. . . . . 8. *Citrus.*

Subfam. RUTOIDEAE Engler

1. **Ruta** Linnaeus, Sp. Pl. 1: 383. 1753; Gen. Pl. ed. 5. 180. 1754.

Heavy-scented perennial herbs, subshrubs [or shrubs]. Leaves alternate, usually glandular-punctate, compound [or simple], odd-pinnate to -bipinnate, with pinnae or pinnules respectively deeply cut (divided) into obovate-cuneate to oblanceolate or oblong segments. Flowers bisexual, 4- or 5-merous, in terminal, panicled cymes with simple or 3-fid bracts. Sepals ± connate at base, persistent. Petals yellow or greenish, glandular-punctate, spatulate-cochleariform with incurved, hooded apex, ± clawed, denticulate [fimbriate or entire], imbricate in bud. Stamens 8–10, in 2 series, the outer (antipetalous stamens) usually somewhat shorter than the inner whorl (antisepalous stamens); filaments filiform, broadened toward the base; anthers oblong. Gynoecium syncarpous, 4–5-carpellate, raised on an intrastaminal, cushion-like, nectariferous disc; stigma small; style central; ovary deeply 4- or 5-lobed, 4- or 5-locular, with [2 to] numerous ovules on axile placentae. Capsule glandular-punctate, 4- or 5-lobed, 4- or 5-locular, [few- to] many-seeded, dehiscent loculicidally inward (adaxially) at apex, [or split into indehiscent segments]. Seeds angled, brown, tuberculate; endosperm fleshy; embryo slightly curved, cotyledons sometimes 2-lobed. (Including *Haplophyllum* A. L. Juss.). LECTOTYPE SPECIES: *R. graveolens* L.; see P. Wilson, N. Am. Fl. **25**: 212. 1911. (Classical Latin name of the plant [since Cicero in literature], related to and questionably derived from Greek, *rhyte*, the name of the plant in Nicander; etymology obscure.) — RUE.

A genus of about 60 species, ranging from Macaronesia eastward through the Mediterranean region to central Asia and eastern Siberia. *Ruta graveolens* L., common rue, $2n = 72, 81$, native to the Mediterranean region but widely naturalized in temperate parts of the Old World, is introduced and more or less naturalized in the eastern United States. There are few reliable records from our area and further data regarding

the distribution of this species in the southeastern United States are very desirable.

The species is proterandrous. The stamens execute peculiar nutation movements during the expansion of the flowers. Pollination agents recorded are small Hymenoptera, Coleoptera, and Diptera. Polyploidy seems to be of frequent occurrence in the genus, and at present diploid, tetraploid, and octoploid species are known. The occurrence of a nonaploid chromosomal race of the otherwise octoploid *Ruta graveolens* has also been recorded. However, no general conclusions can yet be drawn on the basis of the few counts.

The common rue is of ancient culture as an ornamental, spice, and medicinal plant. Because of a volatile oil ("oil of rue") it was formerly used in medicine, but at present, its use is quite limited because of very unpleasant secondary effects. The species should be regarded as ± poisonous. Contact with fresh leaves of the plant produces a dermatitis in some individuals. Poisoning by oil of rue is characterized by gastroenteritis. The Mediterranean *R. chalapensis* L. and some other species have also been used locally in much the same way as *R. graveolens*. The latter and a few other species are cultivated as ornamentals.

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2. **Zanthoxylum** Linnaeus, Sp. Pl. 1: 270. 1753; Gen. Pl. ed. 5. 130. 1754.

Deciduous or evergreen trees or shrubs, often armed with prickles which sometimes become elevated on broad-conical or -pyramidal corky excrescences; bark aromatic. Leaves alternate, odd- or even-pinnate to 1-foliolate; leaflets opposite or alternate, frequently inequilateral, crenulate or entire, glandular-punctate, at least at the margin; petiole and

rachis winged or wingless, unarmed or prickly. Plants dioecious, monoecious, [or polygamous]; flowers small, white to greenish yellow, unisexual [and/or bisexual], in axillary short spikes or cymose fascicles or in terminal, sometimes corymbiform, panicles. Sepals 3–5[10], distinct or ± connate, deciduous or persistent, or apparently wanting. Petals 3–5[8], imbricate [or valvate] in bud. Stamens 3–5[8], distinct, alternate with the petals, rudimentary (staminodial) or wanting (or sometimes transformed into carpels) in ♀ flowers; filaments filiform to subulate; anthers ovate, elliptic to subcircular in outline. Intrastaminal disc small, often pulvinate, or obscure. Gynoecium of (1)2–5 sessile or stipitate, distinct or partially united [very rarely completely connate] carpels, rudimentary in ♂ flowers; stigmas capitate, distinct or connate; styles sublateral, distinct, connivent or connate toward the summit; ovaries usually 1-carpellate and -locular [very rarely ovary compound, 2–5-carpellate and -locular] with 2 collateral, pendulous ovules in each carpel [or locule]. Fruits 2-valved follicles, distinct or connate at base. stipitate to sessile, firm-walled or fleshy, glandular-punctate, with separating (loose) or adherent endocarp, 1(2)-seeded. Seeds obovoid to subglobular [or ± lenticular], black [blue-black, brown, or dark red], shining, with a crustaceous testa and fleshy endosperm, at maturity often hanging from the carpels on slender funicles; embryo axial, straight or somewhat curved, with a short radicle and flat, almost circular cotyledons. (Including *Fagara* L., nom. cons., type: *F. Pterota* L.) TYPE SPECIES: *Z. americanum* Mill. ("Xanthoxylum") (*Z. fraxineum* Willd.); see F. R. Fosberg, Taxon 8: 103–105. 1959. (Name from Greek, *xanthos*, yellow, and *xylon*, wood.) — PRICKLY ASH.

A genus of about 215 species, primarily pantropical, extending with several species into the Temperate Zone of eastern Asia and North America. Two subgenera sometimes regarded as distinct genera are recognized in the present treatment.[2]

Subgenus ZANTHOXYLUM, with unisexual flowers with petaloid [or sometimes sepaloid], 4–5[10]-merous, "simple" perianth in a single series (presumably petals) and 4–5[8] stamens or [1]3–5 carpels, includes about 15 species, primarily of the Temperate Zone of eastern Asia and North America, but with at least two species in Central America. *Zanthoxylum americanum* Mill., common or northern prickly ash, $2n = 68$, 136, a shrub or small tree with odd-pinnate leaves, paired pseudostipular prickles (rarely prickleless) and yellow-green flowers in sessile, axillary, umbellate clusters, expanding before leaves, is the only eastern North American species of the subgenus, occurring from Georgia and Alabama northward beyond our area to North Dakota, Minnesota, Ontario, and western Quebec. *Zanthoxylum mazatlanum* Sandwith is known from

[2] The occurrence of species apparently transitional in the character of the perianth between *Zanthoxylum* and *Fagara* is ample reason to regard both as components of a single genus. See "Taxonomic and Nomenclatural Notes on *Zanthoxylum* and *Glycosmis* (Rutaceae)" in the present issue of this *Journal*.

Mexico; *Z. Williamsii* Standl. and *Z. ferrugineum* Radlk. occur in Honduras and Costa Rica respectively.

Subgenus FAGARA (L.) Triana & Planch. (*Fagara* L.), with unisexual [or both uni- and bisexual] flowers with 3–5[–8]-merous perianth in two series (i.e., sepals and petals), 3–5[–7] stamens and/or 3–5 carpels, includes about 200 species, primarily of the tropics of both hemispheres, four in our area. *Zanthoxylum Clava-Herculis* L., southern prickly ash, Hercules' club, $2n$ = ca. 72, armed trees or shrubs with odd-pinnate leaves and usually 5-merous flowers in terminal panicles, occurs on the Coastal Plain from southern peninsular Florida to Texas and southeastern Virginia, northward to southern Arkansas and Oklahoma. The South American-West Indian *Z. Fagara* (L.) Sarg. (*Fagara Pterota* L.), an evergreen shrub or tree usually armed with pseudostipular prickles, with odd-pinnate leaves having relatively small leaflets and winged petioles and rachises, and 4-merous flowers in short axillary spikes, reaches its northern limit in central Florida and in southern and southwestern Texas beyond our area. The West Indian *Z. coriaceum* A. Rich., a ± prickly tree or shrub, usually with even-pinnate, coriaceous leaves and 3-merous flowers in terminal panicles, is known from southern peninsular Florida and the Florida Keys. The West Indian *Z. flavum* Vahl, yellow-wood, satinwood, an unarmed tree with odd-pinnate, occasionally 3–1-foliolate leaves and 5-merous flowers in terminal panicles, occurs on the lower Florida Keys.

Little is known regarding pollination, but bees and various Diptera have been recorded as the most frequent visitors of the flowers of *Z. americanum*. Nucellar polyembryony has been found in a few species (e.g., *Z. americanum*, "*Z. Bungei* Planch.," *Z. alatum* Roxb.), but probably is of wider distribution within the genus. The few published chromosome counts ($2n$ = 32, 64, 68, 70, 72, 136) indicate polyploidy and perhaps aneuploidy. No interspecific hybrids have been recorded. A modern monograph is highly desirable.

The dried bark of *Zanthoxylum americanum* and *Z. Clava-Herculis*, "toothache bark," "prickly ash bark," or "xanthoxylum," has been applied as a stimulant, tonic, and sialagogue in the United States, and the bark of *Z. alatum* has been used against fever, dispepsia, diarrhoea, and cholera in India. *Zanthoxylum americanum* and some eastern Asiatic species are sometimes cultivated as ornamentals. Various other species have been used for timber, spices, and medicines.

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Subfam. TODDALIOIDEAE Engler

3. **Ptelea** Linnaeus, Sp. Pl. 1: 118. 1753; Gen. Pl. ed. 5. 54. 1754.

Unarmed shrubs or small trees, with bitter bark and foliage disagreeably scented when crushed. Leaves alternate, usually 3-foliolate, rarely 4–5-foliolate, leaflets entire or toothed, glandular-punctate, glabrous to densely soft-hairy beneath. Plants usually polygamous, the flowers bisexual and/or unisexual, greenish or yellowish white, aromatic, in terminal corymbiform, cymose panicles. Sepals usually 4 or 5, distinct, imbricate. Petals usually 4 or 5, relatively narrow, surpassing the sepals, imbricate. Stamens usually 4 or 5, alternating with petals, hypogynous, inserted at base of a disc, very short, with imperfect sterile anthers in ♀ flowers; filaments subulate, hairy in the lower half; anthers ovate-cordate, introrse. Gynoecium syncarpous, usually 2-carpellate, inserted on a low disc in bisexual and ♀ flowers, very small, imperfect (lacking style and with rudimentary stigmas), raised on a conspicuous truncate-pyramidal to subglobular disc in ♂ flowers; stigma capitate, usually 2-lobed; style relatively short and slender; ovary compressed, usually 2-locular and narrowly 2-winged, with 2 superposed ovules (the lower usually sterile) on axile placenta in each locule. Fruit a flat, subcircular to obovate, glandular-punctate samara with 2 broad, thin, reticulate lateral wings completely encircling the indehiscent 2-locular and 1(2)-seeded body. Seeds laterally compressed, semiovate to semilanceolate in outline, acute at apex, rounded at base, dark reddish brown to black, densely papillose and glossy on the surface; seed coat thin, leathery; endosperm fleshy, thin; embryo large, straight, with oblong to ellipsoid cotyledons and short, stoutish superior radicle; germination epigeous. LECTOTYPE SPECIES: *P. trifoliata* L.; see P. Wilson, N. Am. Fl. **25:** 208. 1911. (Classical Greek name of elm, *Ulmus*, transferred by Linnaeus to this genus on account of the similar fruit.) — HOP-TREE, SHRUBBY TREFOIL.

A genus of three (according to P. Wilson) or probably more species,

of temperate North America. *Ptelea trifoliata* L. (including *P. microcarpa* Small fide Wilson), common hop-tree, stinking ash, $2n = 36, 42$, a shrub or small tree, very variable in regard to size, shape, and pubescence of the leaflets and size and shape of fruits, occurs from northern Florida, throughout our area, and beyond to Texas and northern Mexico, Nebraska, Iowa, Michigan, southern Ontario, New York, and Connecticut. Its variant var. *mollis* Torrey & Gray, regarded by Wilson as *P. tomentosa* Raf., with branchlets, lower surface of the leaflets and inflorescences subtomentose, ranges from Georgia to North Carolina and westward to Oklahoma, Arizona, and Mexico. *Ptelea serrata* Small, an irregularly branched shrub with shallowly serrate leaflets, probably belongs with the preceding. *Ptelea Baldwinii* Torrey & Gray, a shrub with leaflets smaller and narrower than in *P. trifoliata*, has been recorded only from northeastern Florida in our area but is apparently conspecific with *P. angustifolia* Benth., widely distributed in the western United States from southern Texas to Colorado, Utah, California, New Mexico, and Arizona, and southward into Mexico.

Vegetative reproduction by root sprouts has been recorded in *Ptelea trifoliata*. The occasional occurrence of 3- or 4-carpellate ovaries, sometimes accompanied by a few additional antipetalous stamens, is noteworthy. Polygamy seems to be a generic character. Although herbarium specimens usually are represented either by male or by female inflorescences, sometimes both bisexual and male flowers occur in the same inflorescence; more rarely a few female flowers (usually terminal) are found in the male inflorescence. Cross-pollination is the rule because of the predominance of unisexual flowers, but self-pollination seems to be possible in the bisexual flowers. Bees, especially short-tongued species, and a few other Hymenoptera and Diptera have been recorded as pollinators. The occurrence of a nucellar embryo has been recorded in *P. trifoliata* (Mauritzon, 1935), but the observations (made on scanty material) need verification. Only two chromosome counts are reported for the genus. No hybrids have been recorded, but, Desai (1960), investigating the cytology of *P. trifoliata* grown in England ($2n = 42$), observed meiotic irregularities resulting in high sterility and concluded a possible hybrid origin for the plant.

Over 60 species of *Ptelea* have been described, but these are apparently not well understood at present, and the reduction of all of them to two or three species is open to question. A modern monograph is urgently needed.

Ptelea trifoliata is a generally known ornamental plant. Its bitter fruits have sometimes been used in brewing as a substitute for hops, hence the English name of the genus. The bark is reputed to possess medicinal properties as a weak tonic.

REFERENCES:

See also under family references DESAI (1960, pp. 29, 30), ENGLER (1931, pp. 302, 303), MAURITZON (1935, pp. 339, 346), URBAN (1883, pp. 397, 398), and WILSON (1911, pp. 208–210).

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4. **Amyris** Linnaeus, Syst. Nat. ed. 10. **2**: 1000, 1367. 1759.

Usually glabrous shrubs or trees with resinous, fragrant wood. Leaves opposite [subopposite or alternate], odd-pinnate, often 3–5[rarely 1]-foliolate, with glandular-punctate leaflets and unwinged [or winged] petioles. Flowers small, bisexual [rarely unisexual], usually 4[rarely 3 or 5]-merous, pediceled, in terminal or axillary panicled cymes. Calyx cuplike, 4-lobed, glandular-dotted, persistent. Petals 4, white, glandular-dotted, imbricate in bud. Stamens 8, in 2 series, inserted at base of a disc or of the ovary; filaments filiform; anthers ovate to oblong, introrse, 2-locular at anthesis. Intrastaminal disc pulvinate, gynophore-like, supporting gynoecium, or wanting. Gynoecium 1-carpellate; stigma capitate to discoid-subcapitate; style very short and stout or wanting; ovary 1-locular, with 2 collateral ovules suspended from the top of the locule. Drupes globular, ellipsoidal to obovate, black [or reddish], often glaucous, dotted with glands, aromatic, oily, the endocarp chartaceous, 1-seeded. Seed pendulous, with thin, membranaceous testa, lacking endosperm; embryo with plano-convex, fleshy, glandular-dotted cotyledons and a short, superior radicle. LECTOTYPE SPECIES: *A. balsamifera* L.; see P. Wilson, N. Am. Fl. **25:** 216. 1911. (Name apparently derived from Greek, *a*, with, abounding in, and *myron*, balsamic juice, resin, with reference to the balsamic properties of the genus.) [3] — TORCHWOOD.

A genus of about 20 species of the West Indies and especially of cis-Amazonian tropical America, extending southward (with one species?) to Peru and northward (with a few species) to Texas and Florida. The South American-West Indian *A. balsamifera* L., with 3–5-foliolate leaves, leaflets dull underneath, puberulous inflorescences, and puberulous, stipitate ovary, occurs in southern peninsular Florida and the Florida Keys. The primarily West Indian *A. elemifera* L., differing from the preceding especially in the glabrous inflorescences and glabrous, sessile ovaries, is

[3] More frequently the Greek prefix *a* has been used in a reverse sense, *without, devoid of, not*. This has led Little (U.S. Dep. Agr. Handb. **41:** 57. 1953) to a different, hardly probable derivation: "not myrrh," "not true myrrh."

also known from southern peninsular Florida and the Keys, and the very similar *A. maritima* Jacq., with stipitate ovaries, has been recorded from Key West. Wilson and Small included this last species in *A. elemifera*, but Urban (1896, 1920) regarded it as distinct.

The genus is, in general, very imperfectly known. The species, especially the West Indian, are closely related, and their delimitation is often weak, sometimes being based on few, questionably specific characters. A modern revision based on field observations, experimental cultures, and cytology is very desirable.

The resinous timber, especially that of *Amyris balsamifera* and *A. elemifera*, is of excellent quality but is scarce and of small size. It is used locally for fuel, torches (fragrant when burned), small cabinet work, and to a limited extent as a source of an oleoresin, Mexican elemi, which is used locally in medicine.

REFERENCES:

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———. *Amyris* L. Symb. Antill. **8**: 323. 1920. [Includes synonymy and general distribution of our spp.]

Subfam. AURANTIOIDEAE Engler

5. **Glycosmis** Corréa, Ann. Mus. Hist. Nat. Paris **6**: 384. 1805.

Unarmed, evergreen shrubs or trees. Leaves alternate [rarely opposite], odd-pinnate, often 1–3(5)-foliolate; leaflets pellucid-punctate, entire [serrate or crenulate], ± inequilateral at base; petiole articulated with the blade in 1-foliolate leaves. Flowers relatively small, fragrant, bisexual, (4)5-merous, with very short, stout pedicels, in rusty-villosulous, spike-like cymes arranged in axillary panicles. Sepals (4)5, nearly distinct [or ± connate], triangular-semicircular, ± fleshy, imbricate. Petals (4)5, elongate, somewhat concave, white, imbricate. Stamens (8)10, the antipetalous shorter than the alternipetalous, filaments flattish [or filiform], dilated upward [or downward] and abruptly narrowed into an acuminate tip; anthers relatively short, ovate-cordate, often apiculate, gland-tipped. Gynoecium 2–5-carpellate, syncarpous, raised on a cushion-like [or cylindrical] nectariferous disc; stigma broad, cushion-like (convex-disciform to semiorbicular), persistent; style often indistinct, short and very stout, merging into a subglobular or ellipsoidal 2–5-locular ovary covered with glands; ovules pendulous, one in each locule. Fruit a relatively small berry with thin pulp, ± globular, sometimes depressed at apex and ± oblique, 1–3-seeded. Seeds without endosperm, ellipsoid to subglobular, with a membranaceous testa; embryo with plano-convex cotyledons and a short

superior radicle. LECTOTYPE SPECIES: *G. arborea* (Roxb.) DC. (*Limonia arborea* Roxb.); see P. Wilson, N. Am. Fl. **25**: 215. 1911.[4] (Name from Greek, *glycys*, sweet, and *osme*, scent, odor, referring to the fragrant flowers of the genus.)

A genus of about 35 species of southeastern Asia, the East Indies, the Philippines, New Guinea, and northeastern Australia. The southeastern Asiatic *Glycosmis parviflora* (Sims) Little (*G. citrifolia* (Willd.) Lindl.), with white or pink subglobular berries, widely cultivated in the warm regions of both hemispheres, has become naturalized in the hammocks of Key West (Small, Manual, 1933; Everett, 1940). Wilson (1911) and some other authors have included this species in "*G. pentaphylla* (Retz.) DC." or "*G. pentaphylla* (Retz.) Corréa."

The present knowledge of the genus is very imperfect, and both taxonomy and nomenclature are complex. Tanaka has studied the genus critically for many years but has not yet published a monograph.

The genus is of no economic importance.

REFERENCES:

See also under family references ENGLER (1931, pp. 316–318), PENZIG (1887, pp. 194–209, *pls. 19–21*), SWINGLE (1943, pp. 153–158), and WILSON (1911, p. 215).

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6. **Triphasia** Loureiro, Fl. Cochinch. 152. 1790.

Evergreen shrubs with paired, or sometimes solitary, axillary spines. Leaves 3-foliolate [or simple], occasionally 1- or 2-foliolate; leaflets relatively small, subsessile, the terminal somewhat larger than the lateral, thickish, without evident reticulation, crenulate to crenate, glandular-dotted; petioles short, puberulous, not articulated with the leaf blade. Flowers 1–1.6 cm. long, bisexual, 3[5]-merous, fragrant, solitary or in 2- or 3-flowered cymes in the leaf axils, pedicels short, minutely 2-bracteolate. Calyx cuplike, 3[5]-lobed, persistent. Petals 3[5], linear to lanceolate-oblong, imbricate. Stamens 6[10] in 2 series; filaments slender, broadened toward the base; anthers small, oblong. Disc ringlike to short-cylindric, encircling the stipelike base of the ovary. Gynoecium 3[5]-carpellate, syncarpous; stigma ± capitate, 3[5]-lobed; style slender, deciduous; ovary ovoid to ellipsoid, narrowed toward the ends, 3[5]-locular, with a solitary ovule in each locule. Berry small, dull reddish orange or crimson, with

[4] See also "Taxonomic and Nomenclatural Notes on *Zanthoxylum* and *Glycosmis* (Rutaceae)" in the present issue of this *Journal*.

glandular-dotted exocarp (peel), mucilaginous, pulpy flesh, and 1–3[–5] seeds. Seeds ellipsoid to subglobular, lacking endosperm, with fleshy or leathery testa; embryo straight, with plano-convex, sometimes unequal cotyledons and small radicle. (Including *Echinocitrus* Tanaka.) TYPE SPECIES: *T. Aurantiola* Lour. (= *T. trifolia* (Burm. f.) P. Wils.). (Name from Greek, *triphasios*, threefold, triple, referring to the usually trifoliolate leaves and trimerous flowers of the type species.) — LIMEBERRY.

A genus of three species, probably native in southeastern Asia, the East Indies, and the Philippines. *Triphasia trifolia* (Burm. f.) P. Wilson, common limeberry, $2n = 18, 36$, apparently indigenous to southeastern Asia and the East Indies, has been recorded as naturalized on the Coastal Plain from Florida to Texas. This species, much cultivated as an ornamental and hedge-plant in the warm regions of both hemispheres, is widely naturalized in the tropics. Flowers with 4-merous perianth and gynoecium sometimes occur in this species.

Cross-pollination by insects seems to be the rule, spontaneous self-pollination being prevented by the position of the stigma which considerably overtops the anthers. Nucellar polyembryony has been recorded in *Triphasia trifolia*. A spontaneous autotetraploid form of this species, with leaves thicker and flowers larger than in the diploid, typical form, has been found. Fruits of *T. trifolia* are edible.

REFERENCES:

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SWINGLE, W. T. New varieties and new combinations in the genera *Clausena*, *Oxanthera*, and *Triphasia* of the orange subfamily Aurantioideae. Jour. Wash. Acad. Sci. **30:** 79–83. 1940. [*T. trifolia* var. *tetraploidea* Swingle, 83.]

7. **Poncirus** Rafinesque, Sylva Tellur. 143. 1838.

Shrubs or much-branched small trees with green twigs armed with stout, axillary thorns often flattened at base; foliage spurs with extremely short internodes developing from dormant buds just above the thorns on the previous year's branches. Leaves deciduous, palmately 3-foliolate; leaflets sessile, shallowly crenulate to serrate above the middle; petiole articulated with the blade, narrowly winged. Flowers fairly conspicuous, 3–6 cm. in diameter, bisexual, subsessile, solitary or in pairs on the preceding season's twigs (just above the thorns). Sepals 4–7, usually 5, distinct, ovate, deciduous. Petals 4–7, usually 5, spatulate to obovate, with claw-like bases, white, soon deciduous. Stamens 20–60; filaments free, unequal in length, slender, broadened toward the base; anthers ovate to

ovate-oblong in outline, gland tipped. Intrastaminal disc annular to shallowly cupular, hairy. Gynoecium 6–8(usually 7)-carpellate, syncarpous; stigma capitate; style short and stout; ovary subglobular, hairy, 6–8 (usually 7)-locular; ovules 4–8 in 2 collateral rows on axillary placentae in each locule. Hesperidium subsessile, globular to pyriform, 3–5 cm. in diameter, dull lemon-colored, fragrant when ripe, finely and densely pubescent, many-seeded; peel (exocarp and mesocarp) soft, 5–10 mm. thick, with numerous oil cavities, rather rough; pulp (forming together with the inner walls of the locules the endocarp of fruits) consisting of elongate, cylindric-conical, slender-stalked vesicles (outgrowths of the inner surface of the tangential walls of the locules) filled with a very acid juice and droplets of acrid oil in the center, and with minute, lateral, irregularly branched appendages (FIG. 1g, h) which presumably secrete a viscous fluid. Seeds lacking endosperm, plump, ovoid, the testa leathery; embryos often several in a seed, differing much in size, with 2 equal or unequal cotyledons and a short radicle; germination hypogeous, the young seedlings at first with bractlike cataphylls, then intermediate forms that soon merge into normal 3-foliolate leaves. TYPE SPECIES: *P. trifoliata* (L.) Raf. (*Citrus trifoliata* L.). (From French, *poncire*, of obscure origin but applied earlier to a variety of citron with large, tuberculate fruits [*C. Medica* var. *tuberosa* Risso], perhaps also to other similar varieties.) — TRIFOLIATE ORANGE.

The single species, *Poncirus trifoliata*, $2n = 18, 36$, native to central and nothern China, has become ± naturalized in our area on the Coastal Plain from Florida to Georgia and Texas. *Poncirus* shows only a few insignificant variations and seems to be the most stable species of the group of "citrus fruits" (including also *Fortunella*, *Eremocitrus*, *Clymenia*, *Microcitrus*, and *Citrus*) which have been cultivated for long periods by man (Swingle, 1943).

The floral biology of the species does not seem different from that of *Citrus*. Both cross- and self-pollination seem to be almost equally effective. Nucellar polyembryony, apparently of an induced type, has been proved. A small percentage of autotetraploids sometimes occurs among nucellar seedlings and those of open pollination. *Poncirus* hybridizes freely with species of *Citrus* and *Fortunella*, producing hybrids which usually are female-sterile but which occasionally produce some fertile pollen. Because of competition with nucellar embryos in a seed (and perhaps from other causes) the sexual embryo, when produced, seldom reaches maturity in most of the *Poncirus* × *Citrus* hybrids. This leads to the development of maternal-type seedlings, seriously interfering with the normal segregation and recombination necessary in plant breeding (Yarnell, 1942). Vigorous, variable trigeneric hybrids, some very complex, have also been produced. The citrangedin, involving *Citrus*, *Fortunella* and *Poncirus*, is extremely resistant to cold and is notable in that it shows clearly traces of all three genera, but is strikingly different from any species of those genera.

Generic distinctions in the Aurantioideae are weak and are much in need of further critical study. Although genetic evidence shows that *Citrus* and *Poncirus* are closely related, the latter has a number of differ-

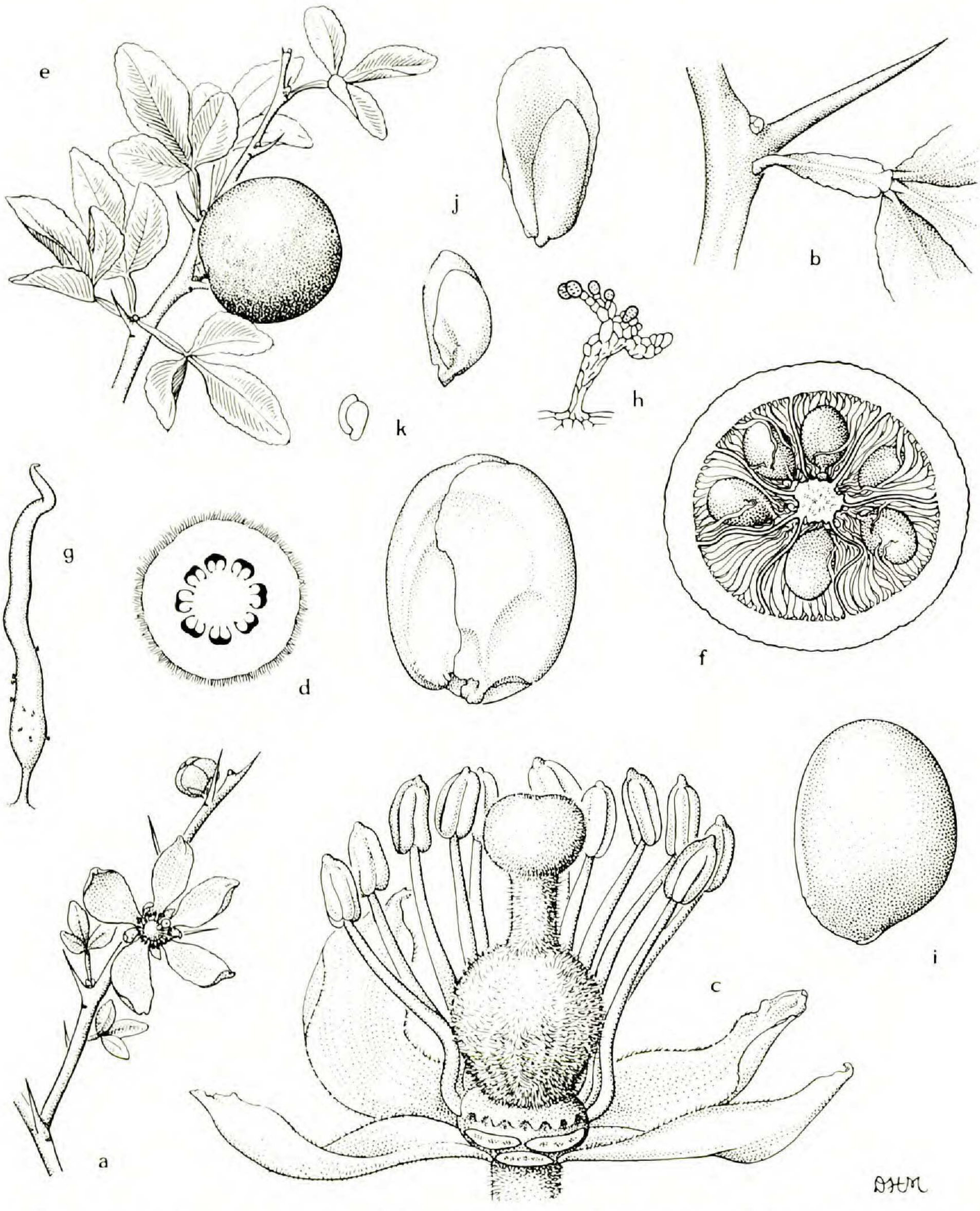

FIG. 1. **Poncirus.** a–k, *P. trifoliata*: a, flowering branchlet, × ½; b, portion of twig, showing winged petiole with base of leaf blade, axillary thorn, and bud, × 1; c, flower (two petals, one sepal removed), showing insertion of stamens, disc, and gynoecium, × 4; d, ovary, diagrammatic cross section, showing ovules on axile placentae, × 6; e, fruiting branch — note foliage spurs. × ½; f, mature 7-locular fruit, showing seeds embedded in pulp vesicles (many omitted), × 1; g, pulp vesicle with minute multicellular lateral appendages, × 3; h, appendage of pulp vesicle (after Penzig, 1887), × ca. 110; i, seed, × 3; j, k, four of nine embryos from a single seed (nucellar polyembryony), × 4 — note mostly unequal cotyledons and different sizes and shapes of embryos.

ential characters: deciduous 3-foliolate leaves; overwintering flower buds covered with bud scales; densely pubescent fruits; pulp vesicles with minute lateral appendages; pith with transverse plates of thick-walled cells; stomata of the green twigs situated at the bottom of deep, narrow pits; seedlings with spirally arranged cataphylls, which merge gradually into foliage leaves, as in *Eremocitrus*; and the presence in immature fruits of the glucoside ponciridin, analogous to hesperidin but not found in *Citrus*. (Cf. Swingle, 1943.) Since the generic problem is very complex, involving a number of other genera, current usage is followed here, and *Poncirus* and *Citrus* are maintained as distinct.

Poncirus has been used more or less extensively in many citrus-producing regions of the world as a rootstock for cultivated citrus fruit trees. The somewhat dwarfing effect on *Citrus* scions is noteworthy. The species is commonly grown as an ornamental in Asia, southern and central Europe, and North America, and is sometimes used for hedges. The fruits have been used in medicine in China. The juice and peel of fruits sometimes are used after special treatment for flavoring in baking and confectionary.

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See also under family references ENGLER (1931, pp. 332, 333), PENZIG (1887, pp. 132–149, *pls. 11, 13, 14*, 'Aegle sepiaria DC.'), and SWINGLE (1943, pp. 366–373).

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8. **Citrus** Linnaeus, Sp. Pl. **2**: 782. 1753; Gen. Pl. ed. 5. 341. 1754.

Glandular, aromatic shrubs or trees, usually with solitary, axillary thorns, the older branches often thornless. Leaves alternate, persistent, 1-foliolate; leaflet subcoriaceous, glandular-dotted, entire or toothed; petiole usually winged and clearly jointed with the blade (except in *C. Medica*). Flowers bisexual, sometimes also unisexual by abortion of the gynoecium, usually relatively large, 2–5 cm. in diameter, often fragrant, solitary or in pairs in the leaf axils or in short, axillary, corymbiform cymes. Calyx shallowly cup-shaped, 4- or 5-lobed. Petals 4–8, usually 5,

linear-oblong, thickish, white, pink, or purplish pink, glandular dotted, imbricate in bud. Stamens 20–60, polyadelphous [or distinct]; filaments linear-lanceolate, subulate upward, white, usually variously connate; anthers oblong or somewhat sagittate. Disc annular to cushion-like, supporting the gynoecium. Gynoecium syncarpous; stigma ± capitate, sometimes slightly lobed; style cylindrical, deciduous; ovary ellipsoidal to subglobular, 8–18(usually 10–14)-locular, with several, usually 4–8, ovules (arranged in 2 rows) on an axillary placenta in each locule. Hesperidium usually large to very large, ellipsoidal and often mammillate at apex or pyriform to subglobular, sometimes depressed at apex; pericarp differentiated into 3 layers: an outer, yellowish-green to orange, leathery exocarp (flavedo) dotted with very numerous oil glands, a middle, thick and spongy, white mesocarp (albedo), and an inner, membranaceous endocarp with juicy, stalked, fusiform, inner outgrowths (pulp-vesicles) filling the locules (segments of the fruit) and forming the "pulp"; the thin, membranaceous partitions (radial walls) of the locules often loosely coherent and easily separated one from another as well as from the spongy, white central column (core) of the fruit. Seeds ellipsoidal to obovoid, plump or flattened, sometimes beaked at apex, usually a few in each locule (segment), the testa leathery; endosperm lacking; embryos 1–several, greenish to white, with fleshy, plano-convex, often unequal cotyledons and short radicle. LECTOTYPE SPECIES: *C. Medica* L.; see P. Wilson, N. Am. Fl. **25**: 221. 1911. (Classical Latin name, originally used for the wood of *Tetraclinis articulata* (Vahl.) Mast., the African sandarac tree, and perhaps other conifers, but transferred to the citron in about the first century of the Christian Era; etymology of the word obscure.)

A polymorphic genus of an uncertain number of species (16–145), of southern and southeastern Asia and Malaysia. Several species with numerous cultivars are widely cultivated and often spontaneous in all warm regions of the world. Five species, *Citrus Medica* L., citron, $2n = 18$; *C. Limon* (L.) Burm. f. (*C. Limonum* Risso), $2n = 18, 36$; *C. aurantiifolia* (Christm.) Swingle, lime, $2n = 18, 19–21, 27$; *C. Aurantium* L. (*C. vulgaris* Risso), sour or Seville orange, $2n = 18$; and *C. sinensis* (L.) Osbeck (*C. Aurantium* [var.] *dulce* Hayne), sweet orange, $2n = 18, 27, 36, 45$, all presumably natives of southern or southeastern Asia, have been recorded as more or less naturalized in our area (primarily southern Florida and the Keys). Accurate and recent data, however, are scanty, and perhaps only *C. Aurantium* and *C. Limon* ("rough lemon") can with some certainty be regarded as extensively naturalized. Seedlings of all the above, as well as of *C. paradisi* Macf., grapefruit, $2n = 18, 27, 36$, are often found along roadsides, at the edges of woods, and in secondary woods in Florida. Further data as to the extent to which such seedlings persist and reproduce themselves are much needed.

Bisexual flowers usually occur regularly in *Citrus sinensis* (also in *C. grandis* (L.) Osbeck, pummelo, *C. paradisi* Macf., grapefruit, and *C. reticulata* Blanco, tangerine). Both bisexual and unisexual (staminate)

flowers are common in *C. Medica*, *C. Limon*, *C. aurantiifolia*, *C. Aurantium*, and some cultivars of other species (polygamo-monoecious species and varieties). Cross-pollination and self-pollination (including pollination between individual trees of a clone) seem equally effective in the formation of embryos and seeds, with some exceptions involving absence or defective development of pollen, or self-incompatibility. Self- or cross-incompatibility has been recorded in some horticultural varieties of different species. Thrips, honeybees, bumblebees, and some other insects attracted by the conspicuous corollas, fragrance, and abundant nectar apparently are responsible for natural cross-pollination and for most self-pollination.

Polyembryony is common in *Citrus*. Gametic (zygotic) polyembryony (gamospermy) seems to be rare, but can arise either by embryonic fission (cleavage polyembryony) or sometimes by the development of two gametophytes (embryo sacs) in the same ovule. Nucellar (somatic) embryony (apomixis, agamospermy) is widely distributed within the cultivated species, apparently lacking only in *C. grandis*. (Some cultivars of *C. Limon* and *C. reticulata* are also mainly monoembryonic.) The number of embryos per seed (1–18) varies with species and variety, and there is no general consistency within the species. Often only a single seedling or rarely more than two or three seedlings develop from a polyembryonic seed. Although nucellar embryos sometimes occur in a fertilized ovule alongside a zygotic embryo, only pollination (not fertilization) seems to be necessary for their formation. The occurrence of autonomous nucellar embryony has not been positively demonstrated. Nucellar seedlings show increased vigor, larger leaves and fruits, and a luxuriant development of spines ("rejuvenation" or "neophyosis"). Parthenocarpy regularly occurs in some cultivars of *C. sinensis* (e.g., navel orange, Satsuma), *C. aurantiifolia* (e.g., 'Tahiti lime,' a triploid), and some others.

The species of *Citrus* generally are interfertile, and their hybrids are ± fertile. Only a few varieties may be cross-sterile, and many inter- and intraspecific hybrids are known. The F_1 progeny of such hybrids usually shows great variability, but less vigor, than nucellar offspring or hybrids from intergeneric crosses (e.g., with *Poncirus* and *Fortunella*). The great variabiltiy of F_1 of inter- and intraspecific hybrids is mainly explainable by parental heterozygosity, which is common. Bud mutants are frequent.

Polyploidy is frequent, triploids (of gametic origin) and tetraploids (somatic autotetraploids) having been recorded in various species, e.g., *C. aurantiifolia* and *C. Aurantium*. Penta- and hexaploids seem to be extremely rare. Aneuploidy and an unbalanced chromosomal complement, $2n = 28$, have been found in a few hybrids.

A mycorrhizal association with an endophytic fungus has been recorded for the genus, but the association seems to be facultative (perhaps ± parasitic), since the formation of root hairs has been observed in young seedlings grown in artificial cultures (Girton, 1927, Hayward & Long, 1942), as well as under field conditions (Bartholomew & Reed, 1943).

There is little unity of opinion on the generic delimitation of *Citrus*.

Although Swingle, who is followed here, regarded *Poncirus*, *Fortunella*, *Eremocitrus*, and *Microcitrus* as distinct genera, some taxonomists include *Poncirus* in *Citrus*, and Burkill (1931) united all of these. Much greater differences exist in the concept of the species. Swingle (1943) recognized 16, at least one, *C. paradisi* Macf., being considered a satellite (or doubtful) species, while Tanaka (1952) accepted 145 species. The difficulties in delimiting the species, subspecies, and varieties of *Citrus* seem to depend, for the most part, on the absence of sterility barriers between groups of related forms and their apparent heterozygosity; but the problem is further complicated by nucellar embryony, by rejuvenation by nucellar progeny of ± senescent varieties long propagated asexually, and by the spontaneous production of autotetraploids.

In addition to morphological and anatomical characters, the chemical composition, especially the presence of certain glucosides in the fruits (e.g., hesperidin and eriodictyol glucoside in *C. sinensis*, those plus hesperidin chalcone in *C. Limon*, hesperidin in *C. Medica*, aurantiamarin, naringin (?), and hesperidin in *C. Aurantium*), seems to be of importance in distinguishing the species. The presence or absence, as well as the number, distribution, and character of the acrid oil droplets in the pulp vesicles of *Citrus* (and relatives) may be of some taxonomic significance.

The diverse uses and application of citrus fruits in the food and beverage industries, in essential oil production and the perfume industry, and as sources of vitamin C and "vitamin P," are well known. The peel (flavedo) of sour and sweet oranges and lemons or the volatile oil extracted from the fresh peel are used in medicine as stimulants, aromatics, and flavoring agents.

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